Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration

Abstract—Aspects of the feeding migration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea (EBS) were investigated by examining the relationship between temperatures and densities of fish encountered during acoustic and bottom trawl surveys conducted in spring and summer between 1982 and 2001. Bottom temperature was used as an indicator of spring and summer warming of the EBS. Clusters of survey stations were identified where the density of walleye pollock generally increased or decreased with increasing water temperature. Inferences about the direction and magnitude of the spring and summer feeding migration were made for five length categories of walleye pollock. Generally, feeding migrations appeared to be northward and shoreward, and the magnitude of this migration appeared to increase with walleye pollock size up to 50 cm. Pollock larger then 50 cm showed limited migratory behavior. Pollock may benefit from northward feeding migrations because of the changes in temperature, zooplankton production, and light conditions. Ongoing climate changes may affect pollock distribution and create new challenges for pollock management in the EBS.

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Walleye pollock (*Theragra chalcogramma*; referred to as "pollock" in this article) migrate seasonally. Such migrations have been described for the northern Sea of Japan (Maeda, 1986; Maeda et al., 1988, 1989; Kooka et al., 1998), Korean waters (Shuntov et al., 1993), the Okhotsk Sea (Shuntov et al., 1987), and the western and central Bering Sea (Fadeyev, 1989; Bulatov and Sobolevskiy, 1990; Efimkin, 1991; Radchenko and Sobolevskiy, 1993; Shuntov et al., 1993; Balykin, 1996). Generally, these authors have described a spring and summer migration from spawning grounds to forage areas (referred to as a "feeding migrations" by many authors) and a winter migration of pollock returning to spawning grounds (e.g., Maeda et al., 1988; Radchenko and Sobolevskiy, 1993). This pattern of migration is believed to occur in the eastern Bering Sea (EBS) where it has received considerable attention (Takahashi and Yamaguchi, 1972; Francis and Bailey, 1983; Pola, 1985; Shuntov, 1992; Shuntov et al., 1993; Stepanenko, 2001), but the evidence for this pattern of migration is sparse. In addition, there is a lack of information on the magnitude of, routes of, and size-dependent differences in seasonal migrations.

Temperature (and other factors closely related to temperature) affects the distribution and movements of pollock. Pola (1985) simulated temperature-induced migrations of pollock in the EBS occurring during May and June. Pollock appear to avoid some temperatures (Swartzman et al., 1994) and prefer environmental conditions that are linked to food availability associated with temperature gradients and fronts along the EBS slope (Swartzman et al., 1995). Water temperature is an especially important indicator of the transition from winter conditions to those supporting a spring bloom of phytoplankton and then zooplankton. In the EBS, the simulated onset of the feeding migration of pollock was delayed in colder years (Pola, 1985).

Annual surveys documenting the spatial distribution of fishes in relation to water temperatures can be used to infer details about their migratory behavior. Using annual survey data, Mountain and Murawski (1992) found that the relationship between the distribution of seasonally migrating species and water temperature could indicate a change in the overwintering location of the fish, or a change in the timing of the spring migration, or both. In the eastern Bering Sea, bottom trawl (BT) surveys and echo-integration-trawl (EIT) surveys are conducted in late spring and summer (Honkalehto et al[1]; Acuna et al.[2]), when water tem-

peratures are generally rising on the eastern Bering Sea shelf (Overland et al., 1999; Stabeno et al., 2001). Interannual variability in climatic conditions and survey timing create variability in mean water temperatures encountered during the surveys (Acuna et al.[2]).

We describe the variability in distribution of pollock with temperature and propose that this variability may be explained by the fact that pollock migrate to feeding grounds during spring and summer. Temperature is used in our study as an indicator of how far into an idealized seasonal warming cycle each survey has occurred. Thus, the distribution of pollock observed in a warm year would be considered to be representative of that seen later in a seasonal warming cycle in a cold year. Generally, feeding migrations appeared to be northward and shoreward, and the magnitude of this migration appeared to increase with walleye pollock size up to 50 cm. Pollock larger then 50 cm showed limited migratory behavior. Pollock may benefit from northward feeding migrations because of the changes in temperature, zooplankton production, and light conditions.

Figure 1

Locations of AFSC bottom trawl stations (dots) and echo-integration survey transects (lines) in the eastern Bering Sea where walleye pollock (*Theragra chalcogramma*) were collected during bottom trawl surveys and echo-integration trawl surveys in spring and summer between 1982 and 2001.

Materials and methods

Data used in this investigation were collected by BT and EIT surveys conducted by the Alaska Fisheries Science Center.

Since 1982, BT surveys have been conducted annually over a standard area of the EBS, at the centers of 20×20 nautical-mile grids (Fig. 1). The corners of the grid block were also sampled in areas surrounding St. Matthew Island and the Pribilof Islands. The same
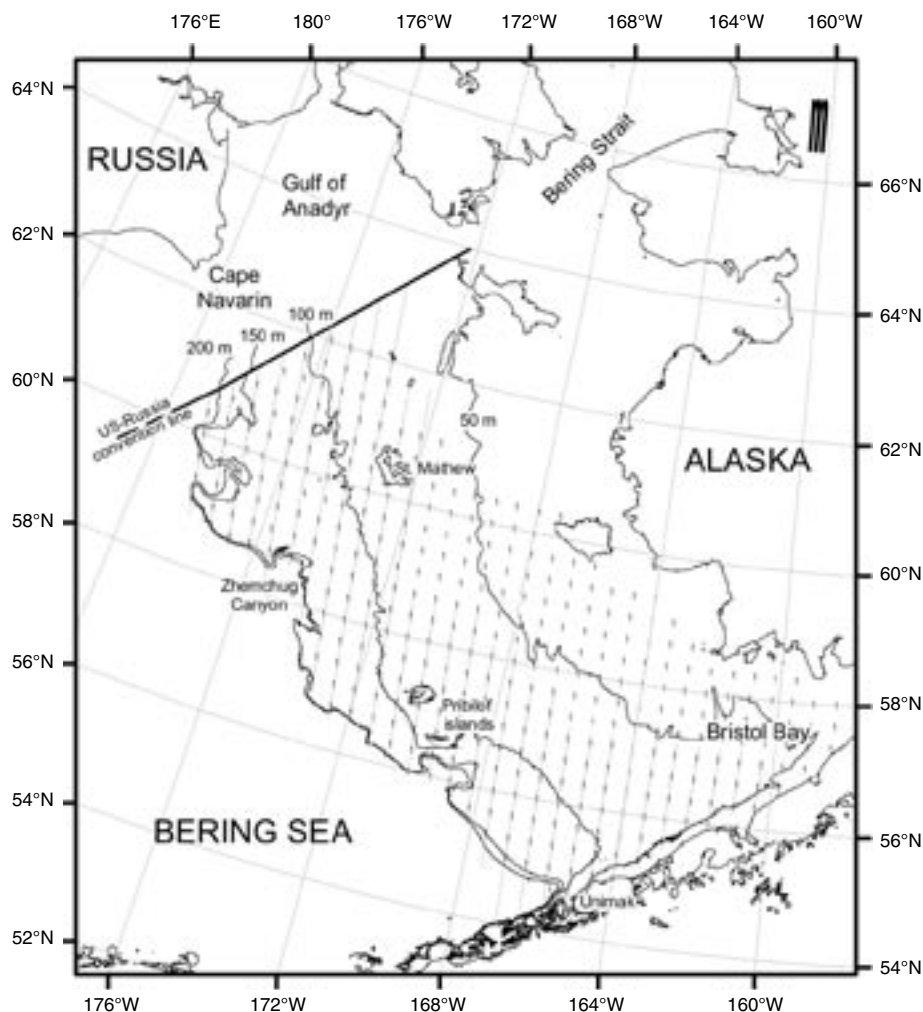
standard trawl (83-112 eastern otter trawl) was used every year (Acuna et al.[2]) and surveys usually began in late May or early June, and ended in August. Surveys always began in the northeastern corner of the Bristol Bay and proceeded westward. Samples were collected by towing for 30 minutes at 1.54 m/s (intended speed). Temperature data were collected during each tow using an expendable bathythermograph (XBT) until 1992 and after 1992 with a micro-bathythermograph (MBT) attached to the headrope of the trawl. Catches were sorted by species and weight; number of fish caught and length-frequency data were collected for each tow.

Echo integration trawl survey transects were designed to coincide with north-south lines of BT stations. Similar to the BT survey, the EIT survey began also in the eastern Bristol Bay and proceeded westward. The time lag between the survey varied from 0 to 30 days. Acoustic data were collected with a Simrad EK500 quantitative echo sounding system. Biological

[1] Honkalehto, T., N. Williamson, and S. de Blois. 2002a. Echo integration-trawl survey results for walleye pollock (*Theragra chalcogramma*) on the Bering Sea shelf and slope during summer 1999. U.S Dep. Commerce, NOAA Tech. Memo. NMFS-AFSC-125,77 p.

[2] Acuna, E., P. Goddard, and S. Kotwicki (compilers). 2003. 2002 bottom trawl survey of the eastern Bering Sea continental shelf. AFSC Processed Report 2003-01, 169 p. Alaska Fish. Sci. Cent., NOAA Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115.

data were collected by midwater trawl, bottom trawl, and Methot trawl (see Honkalehto et al.[1] for details). Pollock length data from trawls were aggregated into analytical strata based on echosign type, geographic proximity of hauls, and similarity in size composition of hauls. Estimates of numbers of pollock by size were derived by scaling acoustic measurements with the target strength-to-length relationship described in Traynor (1996). Temperature data were collected with an MBT mounted on the headrope of the trawl, although many of the profiles did not reach bottom because the trawls usually targeted midwater fish aggregations. For that reason, we elected not to use the temperature data collected during the EIT survey. Because both surveys were conducted at approximately the same time of year, we used the mean bottom temperature from the BT survey as an index temperature for the EIT survey. We used EIT data collected in years 1994, 1996, 1997, 1999, and 2000.

Because of the semidemersal nature of pollock (Bailey et al., 1999a) and assuming that pollock do not dive as a boat and trawl approaches, BT data are assumed to describe the demersal part of the pollock stock within 3 m of the bottom. EIT data represented the midwater part of the stock from 3 m above the bottom to 14 m below the surface. In our calculations, we used two density measures: CPUE in kg/ha for the BT data and biomass (tons) per 20-mile square for EIT data (the term "density" will be used in the present study to refer to both of these measures). Echo integration trawl survey 20-mile squares were centered on the BT survey stations, so that both sets of data could be easily compared (the term "station" will be used here to refer to BT survey stations as well as EIT survey squares). Because of known age-dependent behavioral differences between pollock (e.g., Shuntov et al., 1993; Bailey et al., 1999a), we investigated five different length classes of pollock; up to 20 cm (mostly 1-year-old pollock), 21–29 cm (mostly 2-year-old pollock), 30–39 cm, 40–49 cm, and pollock >50 cm. Because of differences in the year-class strengths between years, we scaled the data by dividing the density data for each station by the average fish density for each year within each length class. Thus, a station with a density value of 1 has an average density for a given year and a station with a value of 5 has a density 5 times larger for a given year.

If the pollock distribution in the EBS is assumed to be dynamic and related to temperature, the relationship between temperature and pollock density will be different at each spatial location. This means that if pollock moved from location A to location B over a period of rising temperatures, we expected a negative relationship between density and temperature in location A and an offsetting positive relationship in location B. To study these relationships in the EBS, we applied a two-step approach. In the first step, we identified possible locations where pollock density may be changing with temperature. In the second step, we identified locations of most significant biomass changes with temperature and quantified these changes.

## First step—identifying areas of change in fish density with temperature

For both types of surveys, we calculated the slope of the linear regression of scaled density against bottom temperature for each station over the time series (e.g., a slope value of 1 indicates an increase of 1 unit of density per degree increase of temperature). Slopes in the range between –0.3 and 0.3 were ignored because they represented areas of low fish density or areas of no significant changes in fish density between years. Each station slope was then plotted on a map to visualize the spatial relationship between these two variables for the BT and EIT surveys.

To contour areas with similar slopes, we interpolated the data using inverse distance-weighted squared interpolation (IDW). This method was chosen because IDW is an exact interpolator, where the maximum and minimum values in the interpolated surface can occur only at sample points and values at all sampling points are true measured values (ArcGIS, Geostatistical Analyst Help, 2003, ESRI, Redlands, CA). Using these maps, we identified the main spatially correlated clusters of stations with positive or negative slopes of the linear regression of pollock density against temperature (Figs. 2 and 3). Stations were assigned to clusters visually by using slope maps that overlapped the stations map. For practical reasons we investigated only clusters with four stations or more. Twenty-eight clusters were identified for BT survey and 17 clusters were identified for EIT survey (Figs. 2 and 3).

Second step—identifying areas of most significant changes in biomass with temperature and quantifying these changes

For each cluster, we calculated mean temperature and percentage of total biomass of pollock present in this cluster in each year. Total biomass and biomass within clusters were calculated as outlined in Wakabayashi et al. (1985). The relationship between mean bottom temperature and percentage of pollock biomass within each cluster was then fitted to a linear regression model. Because the error variances for the BT survey were not constant (variance increased with fish density), we weighted the regression by the inverse of the variance (Neter et al., 1996). For the EIT survey, we made no assumptions about the variance that was due to a small number of observations (only five years of data).

The relative strength of the relationship between the percentage of pollock biomass and temperature within each cluster was characterized by the P-value of the slope (Table 1) (the P-values are not a true measure of statistical significance because the stations were not chosen randomly). Only clusters with the strongest relationships were used in the interpretation of results. Because the number of data points (years) in each analysis was equal within the survey (BT surveys—20 points, EIT surveys—5 points), P-values indicate relative strength of the temperature-biomass relationship. We plotted histograms of P–values for
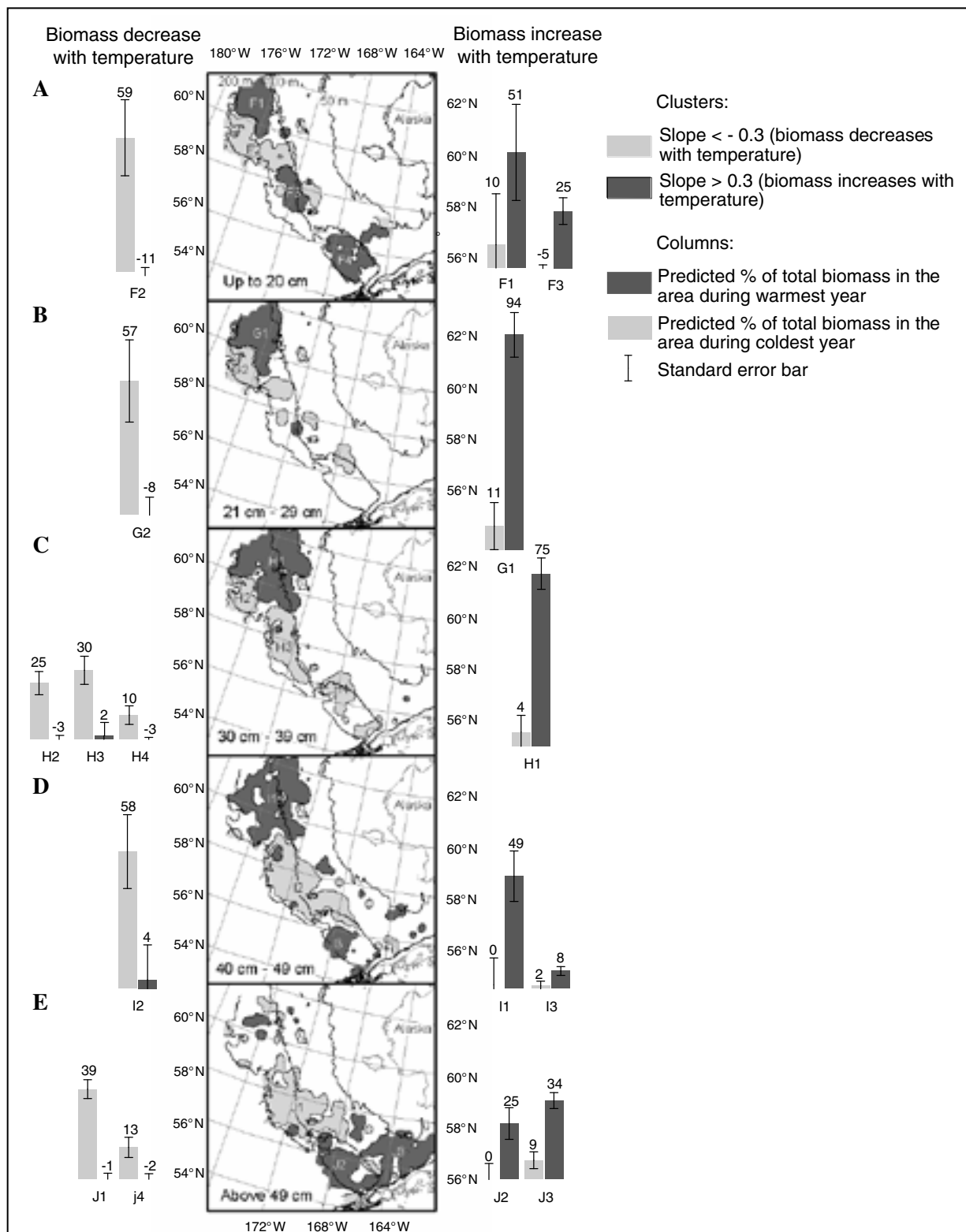
Figure 2

Clusters of positive and negative slopes of the linear regression of pollock (*Theragra chalcogramma*) density (detected by echo-integration trawl survey) when plotted against temperature. Columns represent predicted percent biomass of fish in these clusters within the observed range of temperatures. Predicted percent of biomass is shown only for clusters with the strongest relationship between temperature and fish density with the exception of cluster F1 (see results for explanation). Labels are located at the geographic centers of the clusters.

Figure 3

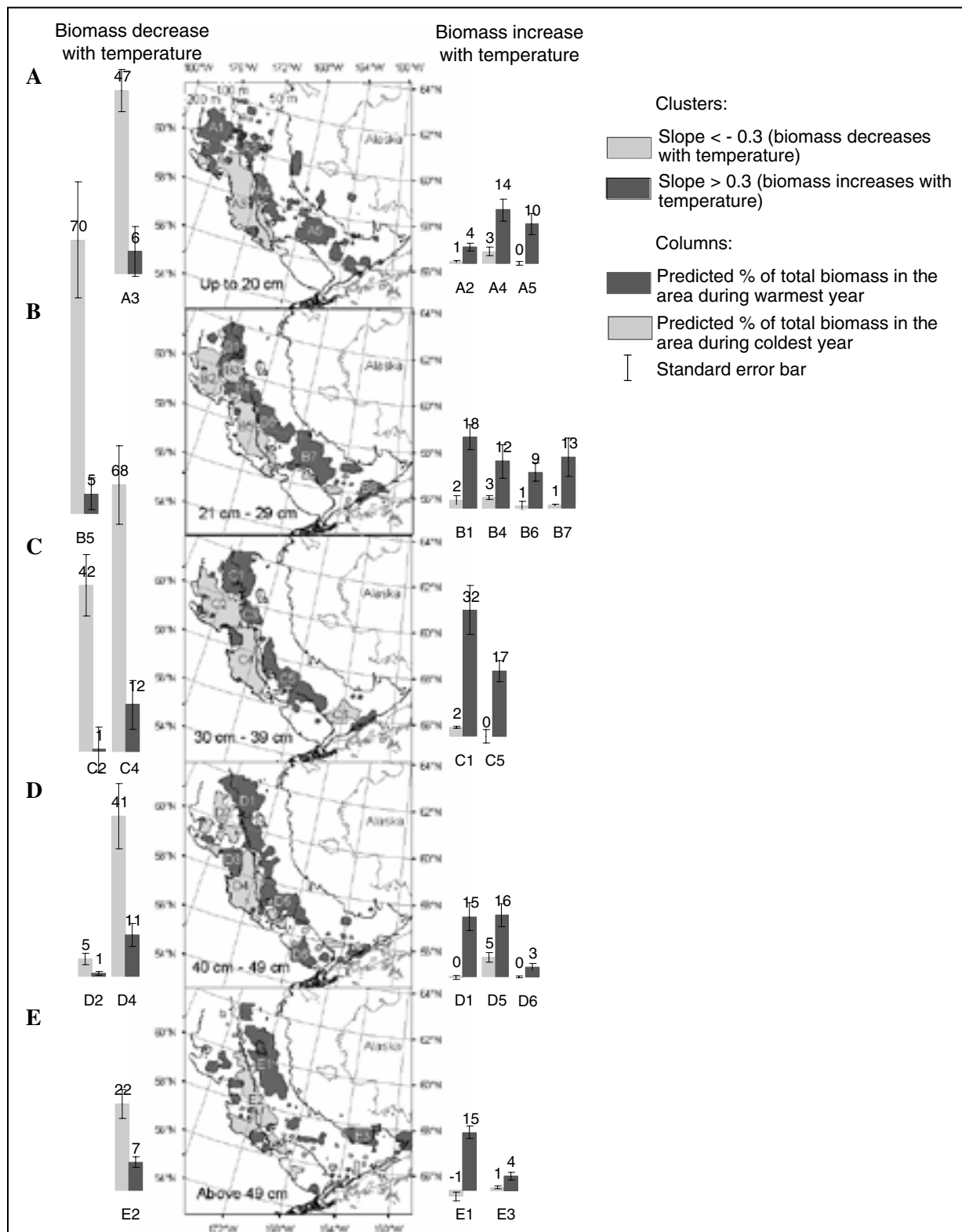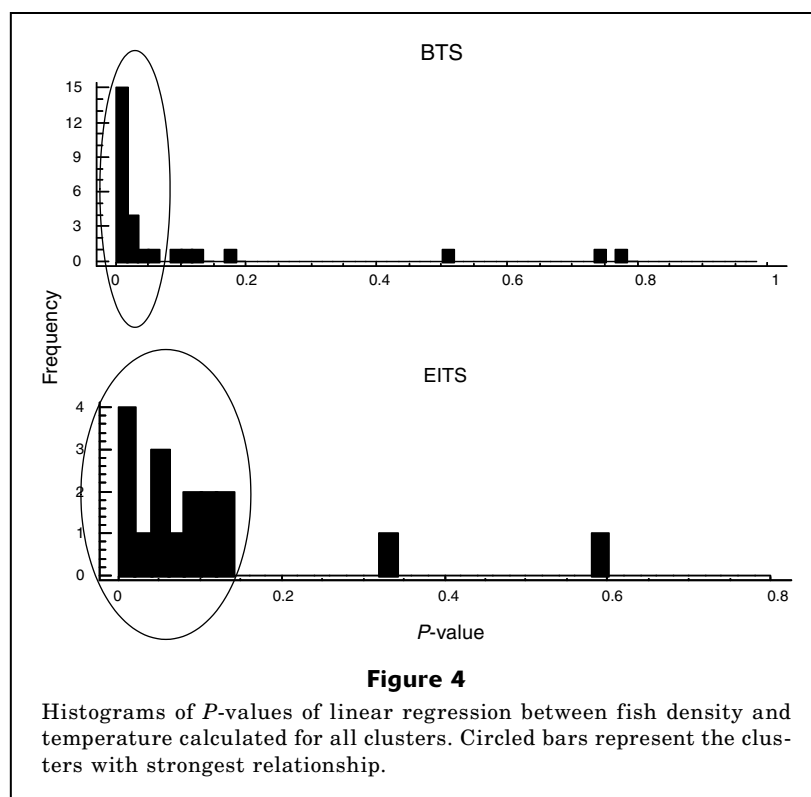Clusters of positive and negative slopes of the linear regression of pollock (*T. chalcogramma*) density (detected by bottom trawl survey) when plotted against temperature. Columns represent predicted percent biomass of fish in these clusters within the observed range of temperatures. Predicted percent of biomass is shown only for clusters with the strongest relationship between temperature and fish density.

Table 1

Results of linear regression analyses and predicted percent of total biomass in each cluster within an observed range of temperatures.

Cluster	Slope	Standard error of slope	Intercept	r^2	P	Percentage at min. temperature	Standard error of min. percentage	Percentage at max. temperature	Standard error of max. percentage
Botton trawl survey									
A1	3.0706	4.579	7.2013	0.024	0.511	8.82	5.07	15.49	4.89
A2	1.1579	0.382	1.6145	0.338	0.007	0.55	0.36	4.31	1.01
A3	−24.0232	6.812	98.8454	0.409	0.002	47.04	5.33	5.79	6.38
A4	3.3081	1.254	2.9747	0.279	0.017	3.14	1.22	13.75	2.84
A5	2.7928	0.837	−0.5577	0.382	0.004	0.08	0.47	10.13	2.65
B1	6.2744	1.655	4.5969	0.444	0.001	1.98	1.21	18.30	3.13
B2	−5.7916	3.445	24.2379	0.136	0.110	21.73	6.37	5.44	3.34
B3	−0.2449	0.839	4.9690	0.005	0.774	4.86	2.07	4.07	0.70
B4	3.6720	1.880	1.4972	0.175	0.066	2.83	0.52	12.05	4.33
B5	−26.2623	7.642	106.0603	0.396	0.003	70.17	14.89	5.08	4.06
B6	1.9462	0.756	2.9913	0.269	0.019	0.62	1.12	9.27	2.31
B7	3.4809	1.408	−0.5292	0.253	0.024	0.77	0.23	13.03	4.94
B8	0.5026	0.350	0.0979	0.103	0.168	0.10	0.44	2.47	1.30
C1	10.9174	2.355	10.7957	0.544	0.000	2.28	0.31	32.32	6.32
C2	−17.9173	5.809	60.4987	0.346	0.006	42.49	7.89	0.51	5.72
C3	1.1807	0.731	1.5962	0.127	0.124	0.84	1.20	4.68	1.26
C4	−26.8246	7.771	116.1162	0.398	0.003	68.32	10.03	12.06	6.27
C5	5.3395	1.413	−3.3847	0.442	0.001	0.11	1.79	16.77	2.65
C6	−1.4934	0.843	6.3588	0.148	0.094	4.77	2.07	0.89	0.28
D1	5.4677	1.368	7.2510	0.470	0.001	−0.15	0.44	15.42	3.55
D2	−1.9038	0.850	5.7227	0.218	0.038	4.50	1.39	0.87	0.45
D3	0.9668	2.954	2.9573	0.006	0.747	4.89	1.28	6.65	4.19
D4	−14.3609	5.356	65.9267	0.285	0.015	41.08	8.45	10.70	2.89
D5	3.6882	1.411	2.7672	0.275	0.018	4.92	1.18	15.81	3.02
D6	2.3974	0.830	−8.0125	0.317	0.010	0.04	0.31	2.60	0.81
E1	4.5778	0.733	6.1399	0.684	0.000	−1.45	1.13	14.86	1.56
E2	−5.7776	1.910	26.8244	0.337	0.007	22.13	3.71	7.32	1.24
E3	0.6479	0.217	0.9447	0.332	0.008	0.91	0.28	3.80	1.01
Echo-integration trawl survey									
F1	16.0479	13.649	−1.2116	0.315	0.324	10.35	21.80	51.49	20.57
F2	−27.5255	9.304	79.2218	0.744	0.059	59.39	14.86	−11.18	14.02
F3	11.7970	3.622	−13.4672	0.779	0.047	−4.97	5.76	25.28	5.46
F4	5.1896	8.463	−3.8753	0.111	0.583	−0.13	13.52	13.17	12.75
G1	32.3770	4.047	−12.0017	0.955	0.004	11.32	6.46	94.33	6.10
G2	−25.5850	10.151	75.6302	0.679	0.086	57.20	16.22	−8.40	15.30
H1	28.0501	4.012	−16.7011	0.942	0.006	3.51	6.41	75.42	6.05
H2	−10.6961	2.999	32.2026	0.809	0.037	24.50	4.79	−2.93	4.52
H3	−11.0388	3.249	38.1076	0.793	0.042	30.16	5.19	1.85	4.90
H4	−5.0998	2.465	13.8907	0.587	0.130	10.22	3.94	−2.86	3.71
I1	19.1934	7.184	−13.8822	0.704	0.075	−0.06	11.48	49.15	10.83
I2	−21.2245	8.449	73.6602	0.677	0.086	58.37	13.50	3.95	12.73
I3	2.3497	1.169	−0.0335	0.573	0.138	1.66	1.87	7.68	1.93
J1	−15.6292	2.465	50.1504	0.930	0.007	38.89	3.94	−1.18	3.72
J2	9.6097	4.374	−6.9678	0.616	0.115	−0.04	6.99	24.59	6.59
J3	9.7424	1.675	1.5600	0.918	0.010	8.58	2.68	33.56	2.53
J4	−5.8055	2.571	17.1422	0.629	0.109	12.96	4.11	−1.92	3.88

Figure 4

Histograms of *P*-values of linear regression between fish density and temperature calculated for all clusters. Circled bars represent the clusters with strongest relationship.

each survey (Fig. 4) and the groups of clusters with the strongest relationships between fish biomass and temperature were chosen for further investigations. These groups consisted of 21 clusters from BT surveys with *P*-values between 0.000 and 0.066 and 15 clusters from EIT surveys with *P*-values between 0.004 and 0.138. Using linear regression models (biomass against temperature), we calculated the predicted percentage of the total pollock biomass for each of these clusters (Table 1) within the temperature range observed during surveys (Fig. 5).

To evaluate a spatial scale on which biomass redistribution occurred for the EIT surveys, we calculated mean distance between clusters of negative and positive slope (Table 2). To obtain these values, we generated 100 random points within each of the clusters and calculated the mean distance between all possible pairs of points from both clusters. We did not attempt to calculate this distance for the BT surveys because of the much more complicated nature of the BT cluster maps.

Results

Northward and inshore shifts in pollock distribution in warmer years were found in the EBS for all length categories. The location and magnitude of these shifts and distance between clusters differed with the survey type and length categories. In the present study we address changes in pollock distribution by length category within each survey.

Table 2

Mean distance between largest echo-integration trawl (EIT) survey clusters. Clusters for pollock >50 cm were not calculated because of low selectivity of the EIT survey for these fish.

Clusters	Mean distance (km)	99% confidence interval (km)
F2–F1	241.3	2.3
G2–G1	217.5	2.5
H4, H3, H2–H1	368.3	4.7
I2–I1	453.7	3.9

Echo-integration trawl survey

The biomass of pollock <20 cm in cluster F2 near Zemchung Canyon at latitude 59°N decreased (with increasing temperature) from about 59% of the total biomass of pollock in the coldest year to 0% in the warmest year (Fig. 2A). This decrease was partially offset by the increase in pollock biomass in area F3, northwest of the Pribilof Islands. The relatively weak relationship (*P*-value=0.324) between pollock biomass and temperature in cluster F1 (north of F2) was caused by the extremely high abundance of <20 cm pollock within cluster F4 during 1997. Therefore the percentage of total

biomass was particularly low in clusters F1, F2, and F3 for that year. In cluster F1 we observed an increase in biomass from 10% to 51%.

For pollock 21–29 cm, changes between cluster G2 and G1 resembled changes between clusters F2 and F1. The percentage of total biomass in these two clusters changed from 57% to 0% and from 11% to 94%, respectively (Fig. 2B).

A slightly different situation was observed for pollock 30–39 cm (Fig. 2C). We identified three clusters of decreasing biomass with temperature: H2, H3, and H4 located, respectively, northwest of Zhemchug Canyon, northwest and east of the Pribilof Islands. Overall predicted biomass change in H2, H3, and H4 decreased from 65% to 2%. The offset for this negative change was found in cluster H1, where we noted a positive change from 4% to 75%.

Areas with decreasing fish biomass for pollock 40–49 cm were located within cluster I2 (Fig. 2D). Biomass decreased from 58% in the coldest year to 4% in the warmest year. We observed temperature-related increases in biomass mostly north of I2 in cluster I1 (0%–49%).

A quite different situation was observed for pollock >50 cm (Fig. 2E). Although pollock of this size seemed to concentrate northwest and northeast of the Pribilof Islands (similar to pollock 30–49 cm) during cold years; in warm years they were found in EIT surveys mainly in the southeast, as opposed to the smaller fish that are found mainly in the north. Results for pollock >50 cm should be treated cautiously because only a very small part of the entire population of pollock this size can be detected with the EIT survey (Ianelli et al.[3]). Because of the benthic habits of pollock >50 cm (Shuntov et al., 1993), most were detected in BT surveys.

Overall, our analysis of EIT survey data indicated a northward temperature-related shift of 50–80% of pollock <50 cm in two major areas. With increasing temperature, the density of pollock <40 cm decreased northwest of Zhemchug Canyon in a large area at 100 m to 200 m depths. Similarly, the density of pollock 30–49 cm decreased northwest of the Pribilof Islands. Offsetting these decreases, pollock density increased in the northernmost area of the survey (close to the U.S.-Russia Convention Line).

Although the direction of the shift was the same for all length categories up to 50 cm, the mean distance between the clusters with negative slopes and clusters with positive slopes increased with fish size (Table 2).

Bottom trawl survey

For pollock <20 cm, we observed a decrease in pollock biomass with temperature in cluster A3 covering the

area west of the Pribilof Islands and north to Zhemchug Canyon (Fig. 3A). We observed an increase in pollock biomass in shallower areas north of Pribilof Island (A4), as well as in the areas of 50–100 m depth east from the Pribilof Islands (A5). The magnitude of change was somewhat smaller than that observed for the EITS survey (see Fig. 3A for details).

For pollock 20–29 cm, we observed a decrease in biomass from 70% to 5% in the area northwest of the Pribilof Islands (cluster B5). A cumulative increase in biomass from 7% to 52% of total biomass was observed in clusters B1 and B4 north of B5, and in clusters B6 and B7 in shallower waters (Fig. 3B). Relatively weak relationships were found between pollock biomass and temperature for clusters B2, B3, and B8.

For pollock 30–39 cm, we observed a temperature-related decrease in biomass in clusters C2 and C4 (42% to 1%, and 68% to 12% accordingly) (Fig. 2C). Increase in biomass was observed in cluster C1 (2–32%) north from C2. Positive change was also observed in cluster C5 (0–17%) within the shallow (<100 m) part of the southeastern Bering Sea shelf.

Clusters D2 and D4 represented areas where we observed a significant decrease in biomass for pollock 40–49 cm (from 5% to 1%, and from 41% to 11%) (Fig. 3D). Increased biomass was detected in cluster D1 located north from D4 and in D5 located to the east of D4 in shallower waters.

Very small changes were detected for pollock >50 cm. Although three clusters had a relatively strong pollock biomass and temperature relationship, the magnitude of biomass changes within the range of observed temperatures was quite small (Fig. 3E).

Overall, as with the EIT surveys, northward shifts in distribution in warmer years were found in the BT survey data for pollock <30 cm. The magnitude of these northward shifts was somewhat smaller (15–30%) than those detected by EIT surveys. In addition, these data suggested an inshore eastward redistribution of pollock in warmer years. Changes for pollock >50 cm were evident but small (in the range of 15%).

Discussion

Inferring seasonal pollock migration from interannual variations in distribution

Interannual differences in the timing of the migration from spawning grounds to forage areas are related to water temperatures. The relationship between temperature and the spatial distribution of a seasonally migrating species could represent either a change in the winter location of the stock or a change in the timing of the migration or both (Mountain and Murawski, 1992). Although the evidence is not conclusive, data suggest that most pollock populations spawn in late winter or early spring in the same locations year after year (Bailey et al., 1999a). For example, large, prespawning aggregations of pollock have been surveyed around

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[3] Ianelli, J. N., T. Buckley, T. Honkalehto, N. Williamson, and G. Walters. 2001. Bering Sea-Aleutian Islands walleye pollock assessment for 2002. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 1–105. North Pac. Fish. Manag. Council, Anchorage, AK.

Bogoslof Island every year since 1988 in the winter (Honkalehto et al.[4]). Further support that temperature is related to the timing of the postspawning migration may come from temperature effects on physiological aspects of spawning. Cold water temperatures may delay the onset of spawning and extend the spawning period of walleye pollock as has been found for another gadid (Kjesbu, 1994) and for flatfish (Lange and Greve, 1997) in the Atlantic.

The surveyed distribution of pollock in warmer years should be more representative of that seen later in a typical spring-summer warming cycle than the distribution of pollock seen in colder years. Bottom temperatures generally increased over the EBS and northern Bering Sea (NBS) during spring and summer (Overland et al., 1999; Khen et al., 2001; Stabeno et al., 2001). Our results show that the warmer the bottom water during spring-summer groundfish surveys, the farther away pollock <50 cm are found from their major spawning grounds. Thus, we interpret areas having lower pollock density with increasing temperature (clusters with negative slope) to be areas from which pollock are emigrating, and areas having higher pollock density with increasing temperature (clusters with positive slope) to be areas to which pollock are immigrating (Figs. 2 and 3).

Routes and directions of the migrations

As the water warms during spring and summer, pollock generally migrate northward, northwestward, and inshore to shallower waters. Larger pollock (>30 cm) begin their feeding migration from spawning grounds. In many areas (white areas—Figs. 2 and 3) we did not detect a significant increase or decrease in pollock abundance in relation to temperature, e.g., in the major pollock spawning area north of Unimak Island (Hinckley, 1987; Bulatov, 1989), and this finding may indicate that migration progressed beyond this area before it was surveyed, even in the coldest years, or that migrations were not pronounced in this area. However, we observed a very large decrease in biomass with increasing temperature in the Pribilof Islands area (i.e., within clusters A3, B5, C4, D4, E2, H3, and I2), which is another important pollock spawning location (Maeda and Hirakawa, 1977; Hinckley, 1987; Bulatov, 1989; Bailey et al., 1999a). An offsetting increase in biomass was observed in the northernmost part of the survey area (clusters B1, C1, D1, F1, G1, H1, and I1) and in shallower waters (clusters A4, A5, B6, B7, C5, and D5), which may indicate that pollock migrate north and inshore during the warming season. Echo integration trawl data indi-

cate that smaller pollock (<29 cm) probably begin their migration from overwintering areas (clusters F2 and G2) located mainly northwest of the Zhemchug Canyon. These results agree with observations made by Bailey et al. (1999b) that small age-0, age-1, and age-2 pollock are distributed farther north than larger age-3 and older pollock. Migrations continued generally northward to the U.S.-Russia Convention Line. The near-bottom part of the pollock population (detected in the BT survey) also migrates northeastward into shallower waters. At this point we cannot describe the exact starting and ending points of migration but only the general direction, because surveys are performed after most of the spawning has been completed, and we lacked data for the NBS, where part of the pollock EBS population is probably migrating.

The direction of movements indicated by the EIT survey data and the BT survey data were somewhat different because of the effect of depth on the availability of pollock to each survey. As pollock migrate into shallower water they become more available to the BT survey and less available to the EIT survey. Therefore the BT survey indicates greater movement into shallower water, whereas the EIT survey indicates greater movement in a northerly direction.

Seasonal migrations by pollock in the EBS are broadly recognized as occurring but have not been well substantiated; however, most of the general observations and descriptions are in agreement with our results. It is generally recognized that the feeding migration of some EBS pollock takes them northwestward beyond our survey area and into Russian waters (Shuntov et al., 1992; 1993; Stepanenko, 2001). Pola (1985), in her numerical simulation of pollock migrations in the EBS identified two types of pollock feeding migration. One was temperature induced in the northward direction, and the other was seasonal in the northeastern direction toward shallower waters. Shuntov et al. (1993) considered migrational activity to start with the onset of sexual maturity, but our findings indicate that immature pollock do undergo feeding migrations in a northwestward direction, but over shorter distances than those traveled by mature pollock. Stepanenko (2001) also recognized migration by immature pollock. Only a few pollock tagged in the EBS have been recovered (Yoshida, 1985), but the relationships between the release and recovery locations are consistent with our findings of a northwestward feeding migration during the spring and summer over most of the EBS shelf and a northeastward migration into shallower water on the southeast EBS shelf.

Length-based differences in migration patterns

Our analysis of the EIT surveys indicates that the migrations of pollock <30 cm are shorter than those of pollock 30–50 cm. The distance pollock need to cover from clusters F2 and G2 to clusters F1 and G1 (241.3 km and 217.5 km) is much shorter than the distance to be covered by larger fish from clusters H4, H3, H2,

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[4] Honkalehto, T., N. Williamson, D. Hanson, D. McKelvey, and S. de Blois. 2002b. Results of the echo Integration-trawl survey of walleye pollock (*Theragra chalcograma*) conducted on the southeastern Bering Sea shelf and in the southeastern Aleutian Basin near Bogoslof Island in February and March 2002. AFSC Processed Report 2002-02, 49 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115.

and I2 to clusters H1 and I1 (368.3 km and 453.7 km, respectively). Similar size-dependent differences in the distance of seasonal migrations were reported for Pacific hake (*Merluccius productus*), another gadoid from the north Pacific (Dorn, 1995). These observations may support the length-based hypothesis of Nøttestad et al. (1999) for feeding migrations in pelagic fish. Focusing on the energetic cost-benefit relationship of long distance migration, they concluded that migration distance is a function of length, weight, and age. Smaller fish may undergo shorter feeding migrations because the energetic cost of migration can exceed their total energy intake resulting from the of greater hydrodynamic drag associated with smaller fish size.

Migrations of the largest pollock (>50 cm), detected from the BT survey data, were of much lower magnitude then those of smaller fish. Our models indicate that only about 15% of fish in this length category move between clusters in the northeastern direction toward shallower waters. These small changes detected in BT data contradict those seen in EIT data. Whereas a small northward shift in biomass (mostly from cluster E2 to cluster E4) was detected with BT data, a southeastward shift was detected with EIT data. However, because the EIT survey is not well suited for estimating the distribution of pollock >50 cm, we are inclined to put more weight on the BT data to explain temperature-related changes in biomass distribution for this length category. Larger pollock (>50 cm) appear to change their migratory behavior. Shuntov (1992) noticed that the distribution of larger pollock (>54 cm) fundamentally differs from that of smaller pollock and that larger pollock are more benthic in behavior and feeding. Stepanenko (2001) did not observe any migrations to the Russian zone for pollock six years or older. We propose that the difference in the migratory behavior between pollock <50 cm and pollock >50 cm is linked to a well-known shift toward a diet of fish with increasing pollock size (Bailey and Dunn, 1979; Dwyer et al., 1987).

Why do pollock migrate?

Pollock feeding migrations in the EBS may be driven by a combination of four factors: temperature, zooplankton production, currents, and length of daylight.

Changes in the water temperature may affect pollock migrations. Bottom water temperature over the Bering Sea shelf rises between April and September (Pavlov and Pavlov, 1996; Overland et al., 1999; Khen et al., 2001; Stabeno et al., 2001). Our results indicate that with rising temperature pollock generally migrate northward and inshore. Pollock appear to avoid temperatures below 0°C (Swartzman et al., 1994); therefore a seasonal increase in temperature above 0°C can open new geographic areas for migration. Temperature was presented as one of several important stimuli affecting fish movements by Harden Jones (1968) and by Wielgolaski (1990), who noticed that capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*) in the Barents Sea migrate

north towards a preferred temperature, either directly to satisfy metabolic requirements, or indirectly, as when attracted by food organisms.

Seasonal patterns in zooplankton production and prey availability largely coincide with seasonal patterns in pollock migration and distribution. The role of food availability in driving fish-feeding migrations has been described for other zooplanktivores such as Pacific hake (Dorn, 1995), Atlantic herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*) and capelin (Nøttestad et al., 1999). In the Bering Sea, the abundance of zooplankton is high on the EBS and NBS shelf throuout spring and summer, but it remains high in autumn only in the NBS (Springer et al., 1989; Chuchukalo et al., 1996; Coyle et al., 1996). Copepods and euphausiids are major prey groups for pollock during spring and summer in the northwest area of the EBS shelf, but in autumn, 30–49 cm pollock increase their feeding on fish and decapods (Dwyer et al., 1987) which may be related to a decrease in the availability of these prey (Willette et al., 1999) in this area. Further north in the Navarin-Anadyr area, copepods and euphausiids remain major prey components in the diet of pollock <50 cm through summer and autumn (Shuntov et al., 2000). The migration pattern of pollock indicates they may follow their food supply as the production and abundance of zooplankton proceeds northward. Pollock larger than 50 cm do not undergo northward feeding migrations because small pollock, other fish, and benthos are the main components of the diet (Dwyer et al., 1987; Yoshida, 1994; Shuntov at al., 2000).

In the area of pollock migrations northwest of Pribilof Islands current speeds are in the range of 1–5 cm/s at the 100 m depth and they generally run in the northwest direction (Stabeno et al., 2001). Current direction coincides with the direction of pollock migrations, so that the cost of the migration may be offset by swimming in the same direction as the transporting current (Nøttestad et al., 1999). Water currents can also influence fish migration indirectly by providing visual stimuli arising from the moving background (Harden Jones, 1968) or by transporting food. Springer et al. (1989) suggested that the transport of zooplankton by the northwest current may cause greater levels of zooplankton concentration in the NBS. Because of the lack of data on current speed, he speculated that a current velocity in the range of 20 cm/s was needed to explain these high levels of zooplankton in the NBS if the high levels of zooplankton are based only on currents. The latest observations of current on the Bering Sea shelf do not support these hypotheses (Stabeno et al., 2001). However northwestern currents may contribute to higher zooplankton biomass in the NBS.

Nøttestad et al. (1999) suggested that light conditions may play a role in fish feeding migrations because during summer day-length increases the farther north fish travel, thus potentially increasing feeding duration for pelagic visual predators. Pollock are visual predators and light conditions affect feeding efficiency of pollock

(Ryer and Olla, 1999; Ryer et al., 2002); therefore it may be that longer days at northern latitudes make a northward feeding migration beneficial by possibly providing an extended window of search time if the pollock happen to be in a locally depauperate area. However, day-length remains long enough in the entire Bering Sea for pollock to feed to satiation, and their gastric evacuation rate is slow (Dwyer et al., 1987), making the need to entirely fill their stomachs every day very unlikely.

Figure 5

Bottom water temperature contours during the bottom trawl survey in the coldest year (1999—upper map) and warmest year (1996—lower map).

At this time it is impossible to assess which factor is most important in driving pollock migrations, but in summary we can conclude that pollock, as visual pelagic predators, benefit from northward feeding migrations during seasonal warming. Because three of the factors (excluding current) are similar throughout the Northern Hemisphere, we should see similar migration patterns for other pelagic fish of the north. Other examples include Pacific hake migrating along the North American west coast from California to British Columbia (Francis and Bailey, 1983; Dorn, 1995). Herring in the Norwegian Sea undergo seasonal feeding migrations in the northwestern direction from the south-central coast of Norway to the areas located northeast of Iceland (Ferno, 1998). Blue whiting, mackerel, and capelin from the north Atlantic undergo northward feeding migrations (Nøttestad et al., 1999). Pacific saury (*Cololabis saira*), chub mackerel (*Scomber japonicus*), Pacific sardine (*Sardinops sagax melanosticta*), and Japanese anchovy (*Engraulis japonicus*) from the western North Pacific are reported to migrate northwards during the summer (Novikov, 1986). Capelin, Atlantic cod, and haddock in the Barents Sea migrate north towards a "preference" temperature during summer (Wielgolaski, 1990). All these species have characteristics similar to those of Bering Sea pollock—that is, a pelagic or semipelagic life style, a diet of zooplankton, winter or spring spawning activity, and feeding migrations that take place during spring and summer.

Why is temperature important?

Temperature may affect the proportion of the stock that is in the standard EBS survey area. Ianelli et al.,[3] using population modeling, estimated that fewer pollock were detected during the BT survey in the EBS with increasing temperature, and fewer pollock would indicate that pollock are probably leaving the survey area during seasonal migrations. We conclude that a significant part of the EBS pollock population migrates into the Navarin-Anadyr area, which can have an impact on the way the EBS stock is managed. We should account for landings of pollock in the Navarin-Anadyr area, estimate how much of these landings include pollock from the EBS stock, and use this estimate in determining the EBS total allowable catch. Further research is needed to quantify the proportion of the EBS stock migrating into the Russian fishing zone and to estimate the number of pollock caught there. Stokes[5] suggested that the biomass estimates from the NBS are in the range of 0.5–1.0 million
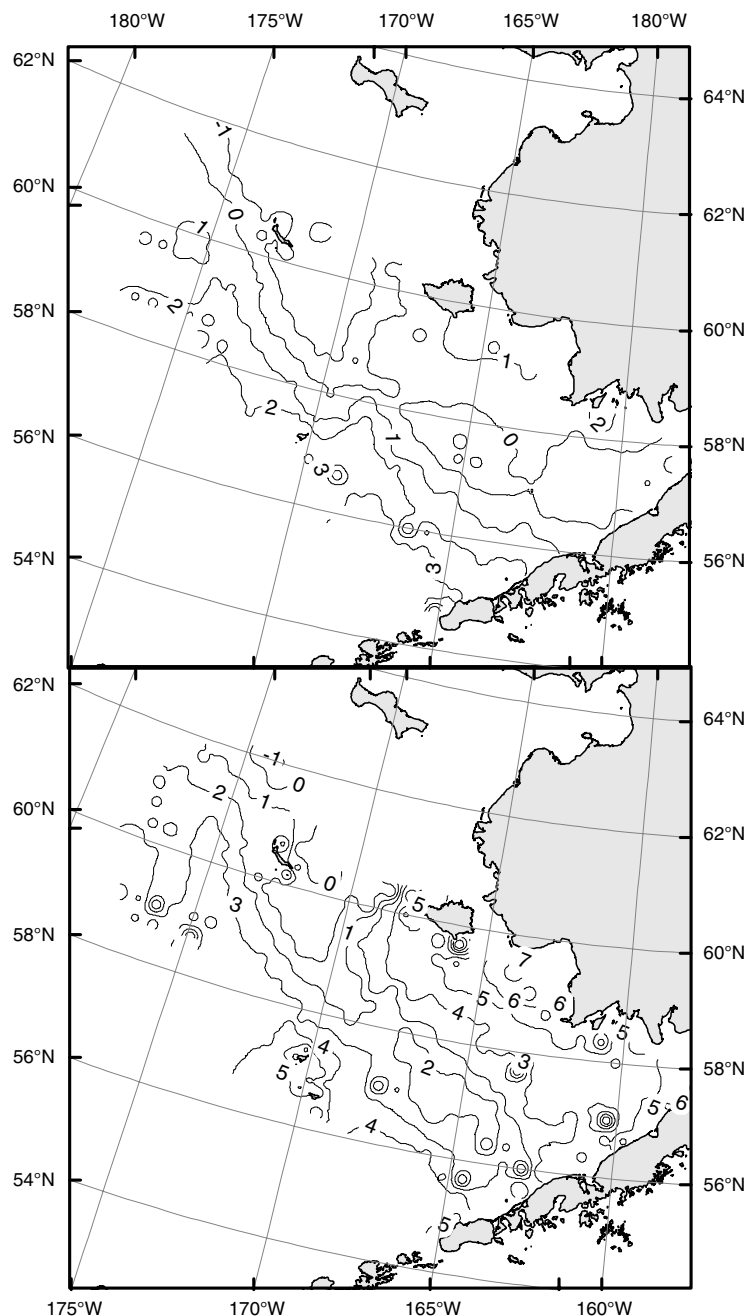
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[5] *See next page for footnote text.*

metric tons per annum and the exploitation rate is in the range of 0.5 million metric tons (50–100% of the total estimate).

Ongoing climate changes may affect pollock distribution between the U.S. and Russian EEZs. Stabeno and Overland (2001) reported a shift toward an earlier spring transition in the Bering Sea. This can affect the starting time of pollock migrations and the length of time fish spend in the Russian EEZ, increasing the availability of fish to the Russian fleet. This situation should encourage us to closely monitor changes in migration patterns of pollock in the Bering Sea.

Significant bias or error variation may be caused by the interaction of fish movement with survey protocol. For even relatively low fish migration velocities (<0.5 m/s), bias in estimated fish biomass can be very large (McAllister, 1998). Therefore, fish migration vectors should be estimated to minimize the bias created by not taking into account these migrations in biomass estimates.

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